



Examensarbete i ämnet biologi

2013:1

Site fidelity of a migratory species towards its annual range

Peter Lojander



©Anders Wittenström



Examensarbete i ämnet biologi

2013:1

Site fidelity of a migratory species towards its annual range

Ortstrohet hos en migrerande art till specifika delar av dess hemområde

Peter Lojander

Keywords: calving, rutting, stopover site, migration, habitat selection, moose (*Alces alces*), ungulates, Sweden

Handledare: Navinder J Singh and Göran Ericsson
Examinator: Jean-Michel Roberge

30 hp, A2E
Kurskod EX0708

SLU, Sveriges lantbruksuniversitet
Fakulteten för skogsvetenskap
Institutionen för vilt, fisk och miljö

Swedish University of Agricultural Sciences
Faculty of Forestry
Dept. of Wildlife, Fish, and Environmental Studies

Umeå 2013

Abstract

Site fidelity, the behaviour of animals to return to areas where they have been before is a common trait in many species. The Scandinavian moose is known to show fidelity to its range, but to what extent, is little known. The landscape in Sweden changes in a predictable and unpredictable way and hence gives the opportunity to test the existence of fidelity. I used the kernel Brownian bridge method to estimate the home ranges of individual moose over consecutive years and estimated the overlap at the home range level. I also used Euclidian distance to look on calving site fidelity. The moose in Sweden show fidelity to the different parts of their annual range at different levels. The overall pattern is that fidelity towards seasonal range increased with increasing latitude in winter, with a reversed pattern in summer, but the southern populations of moose show high fidelity, all year round. The calving site fidelity also follows the pattern of high fidelity in the south and lower fidelity to the north. This could be explained by the different movement strategies and the predictability of resources vital to the moose across the landscape. The increased knowledge could be used to better manage the Swedish moose population and provide information of the causes of fidelity.

Sammanfattning

Ortstrohet, beteendet när djur återkommer till ett tidigare använt område, är ett vanligt hos många djurarter. Den skandinaviska älgpopulationen visar trohet till olika delar av sitt hemområde. I Sverige förändrars landskapet på ett förutsägbart såväl som oförutsägbart sätt och ger således bra förutsättningar för att testa några påstående gällande ortstrohet. Jag använde mig av en kernel Brownian bridge metod för att beräkna hur hemområdena ser ut från år till år och beräknade sedan hur mycket hemområde år ett överlappar hemområdet år två. För att titta på kalvningsplatstrohet använde jag mig av de euklidiska avstånden mellan två års kalvningsplatser. Det övergripande mönstret är att älgar visar trohet till alla delar av sitt hemområde i olika grad. Ett annat tydligt framträdande mönster är en ökad trohet till vinterområden ju längre norrut du kommer. Detta kan antagligen bindas till fördelningen av bete i landskapet och de migrerande rörelsemönstren. I de södra delarna av landet är troheten till hemområdena alltid hög. Detta beror antagligen på de små hemområdena tillsammans med den höga födotillgången och den mer stationära livsstillen. Trohet till kalvningsplatser är högst i de södra delarna av landet, troligtvis beror detta på den högre nivån av mänsklig aktivitet i området. Resultatet från denna studie kan användas för att förbättra den svenska älgförvaltningen och ge värdefull information om orsakerna bakom ortstrohet.

Introduction

Site fidelity

Site fidelity is the behaviour of animals to return to an area where they have previously been (Switzer 1993). The return of the birds in the spring in the northern hemisphere or the large herds of wildebeest that arrive to the same area during the rainy season are both connected to site fidelity. This behaviour is a common trait and has been seen in many taxa (Greenwood 1980). Fidelity might occur due to different reasons, breeding sites fidelity to leks or swarming sites has been seen in sage-grouse and bats (Schroeder & Robb 2003; Furmankiewicz & Altringham 2007) or to the calving areas of grey seal (Pomeroy et al. 2000). Animals may also show fidelity towards migratory paths and seasonal ranges as in caribou and wildebeest (Faille et al. 2010; Morrison & Bolger, 2012). There are also animals showing fidelity to their entire home range as logger head and green turtles (Broderick et al. 2007). But animals do not only show fidelity to a particular range but also to a more specific area of the range as feeding sites (Irons 1998).

The underlying reasons for fidelity are to increase survival and reproduction through increased knowledge on where to find food and safety (Schieck & Hannon 1989, Cameron et al. 1992). Animals living in an unpredictable environment may benefit from site fidelity by knowing the distribution of these key elements and further select areas where these are present (Norbury et al. 1994, Switzer 1993). Fidelity may affect both the demography and the population dynamics, and affect the resilience of a population (Morrison & Bolger 2012). In a population with a high degree of fidelity to leks the structure will create genetically distinct sub populations as the gene flow between the sub populations decreases (Esler 2000).

Conservation and Wildlife management

Fidelity can as said above, effect individuals and populations in different ways and might have long lasting effects on the population and individuals showing fidelity. In addition, the knowledge of how, where and when animals show fidelity can be used for conservation and management (Bolger et al. 2008). The knowledge of where the leks, calving sites, migration routes and seasonal ranges occur can be used to protect the animals during these phases (Singh et al. 2010). The knowledge of fidelity to migratory routes can be used in infrastructure projects to anticipate the usage of game-passovers as animals tend to reuse these areas (Sawyer et al. 2009) or to reduce wildlife vehicle-collisions with humans (Neumann et al. 2012). The knowledge of site fidelity can also be used to improve habitat and food availability. Supplementary feeding strategies can also be designed using the knowledge of site fidelity (Sahlsten et al. 2010). On a management level the knowledge of fidelity within a species can be used to set specific hunting quotas for areas during short time periods.

Moose and site fidelity

The moose (*Alces alces* L). is the largest Cervide and has a circumpolar distribution that is restricted by temperature in the south. In Sweden the moose population is dense with density of about 0,2-2 moose/km² (Lavsund et al. 2003). It can utilise a wide range of habitat but prefer a broken landscape with lots of wetland and lakes and young tree stands

(Maier et al. 2005, Jensen 2004). The moose utilise the same area for browsing and resting (Thompson & Vukelich 1981) and as one of the main browser in the northern hemisphere it can have large effects on the vegetation (Persson 2003). Moose exhibit a whole spectrum of movement strategies from sedentary to migratory and from dispersing to nomadic and may change from one to the other to better cope with their surroundings (Singh et al. 2012). A common trait in migrating animals are that of stopover sites where the animals stay for a while to rest or feed to have a better chance to complete the next stretch of migration. The stopover sites can also be places where the animal awaits the greening to get the best browsing possible. This trait is usually seen in birds (Taylor & Bishop 2008; Buchanan et al. 2012) but has also been reported in terrestrial mammals such as pronghorn and mule deer (Wiseman et al 2006, Sawyer et al. 2012).

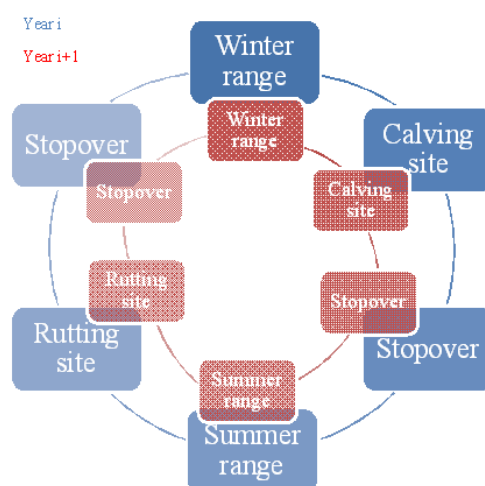


Figure 1. The areas that the moose can show fidelity towards and the overlap between consecutive years.

The moose of Scandinavia are known to show fidelity to different parts of their home range, as summer range (VanBeest et al 2010), winter range (Sweanor & Sandgren 1989) and calving sites (Tremblay et al. 2007). No studies have yet looked at fidelity across entire annual range and throughout the migratory cycles. For example, fidelity towards stopover and rutting sites including calving sites and seasonal ranges.

In the northern hemisphere the landscape changes both in a predictable and an unpredictable way across both space and time. These changes determine the availability of food, distribution of competitors and predators but also climate changes. In predictable environment individuals synchronize their movement and follow a migratory movement strategy (Mueller et al. 2011, Singh et al. 2012). To increase fitness (i.e. survival and reproduction), these individuals might show fidelity to the different parts of their home range (Figure 1). Alternatively, where the landscape change in an unpredictable manner individuals benefit from following other strategies as nomadic or sedentary (Muller et al 2007; Fryxell et al. 1987). These strategies will affect the fidelity in two different ways as nomadic animals won't show fidelity but sedentary will show a high degree of fidelity. There is large variation in climate across Sweden, which in turn drives large changes in the variation of food availability. But the climate aren't the only thing that changes, road density and hunting pressure follow a gradient from low to high from the north to the south. The reverse pattern is present in the large carnivores; mainly bears were the highest densities are found in the north (Appendix 3, Singh et al. 2012).

The proportion of migratory moose changes in a predictable way with a decrease in migratory individuals occurring from the north to the south in response to the changes in snow cover, vegetation period and temperature (Singh et al 2012). Considering this variation across the landscape, site fidelity should be higher in the north compared to south (Figure 2).

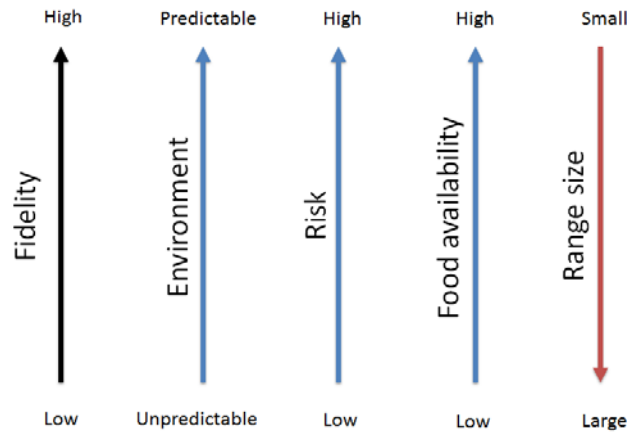


Figure 2. This figure represents the assumptions towards explaining fidelity. Fidelity should increase with predictability of the environment (marked seasonal changes), higher risk, and food availability and decrease with individual / species range size (when species are resident). In a landscape where the environment is unpredictable animals will select for areas where the most predictable conditions are found.

Predictions

In reference to Figure 2, I predict the following for Swedish moose:

1. Site fidelity will be high in the southern latitudes. This due to the year round high food availability. The high levels of anthropogenic risks and the unpredictable landscape. These characteristics will drive the animals to select areas that are more predictable away from human disturbance and have the highest amount of browsing available.
2. In the northern part of Sweden as the landscape and environment is predictable animals will select for areas where food and cover are more abundant. During winter the behaviour to select these areas is more important and this will lead to higher fidelity.
3. Calving site fidelity will be high in regions where risk is high. Risk can be that both from predation and of human disturbance. As anthropogenic risk is more stationary in areas where humans are abundant this will increase the site fidelity. There are two way that predation might affect the selection of habitat of the moose either the moose select for safe areas, this result in high levels of site fidelity. Or the moose move around to avoid predation, this leads to a lower level of fidelity.

Methods

Study area

Sweden is part of the boreal zone and has an elevation from sea level to about 2000 meters over sea level. The annual mean temperature is between 2 to 3 degrees Celsius. Sweden is covered by snow between 50-225 days of each year with a gradient from the coast to the mountains as well as from south to north (SMHI 2013, Appendix 3). It is a long stretched country that spans over 1572 km from the north to south (56-69°N) and has a breadth of 499 km from east to west (10-24 °E). The total land area is 40,8 milj. hectares of this 30,78 milj. hectares are covered by forest (FAO 2013). The forest mainly consists of Scots pine (*Pinus Sylvestris*), Norwegian spruce (*Picea Abies*) and Birch (*Betula Pendula*, *Betula Pubecens*). In the southern parts of the country different kinds of broadleaf trees are found mainly Beech (*Fagus Sylvatica*) and Oak (*Quercus Robur*) (Skogsstyrelsen 2012).

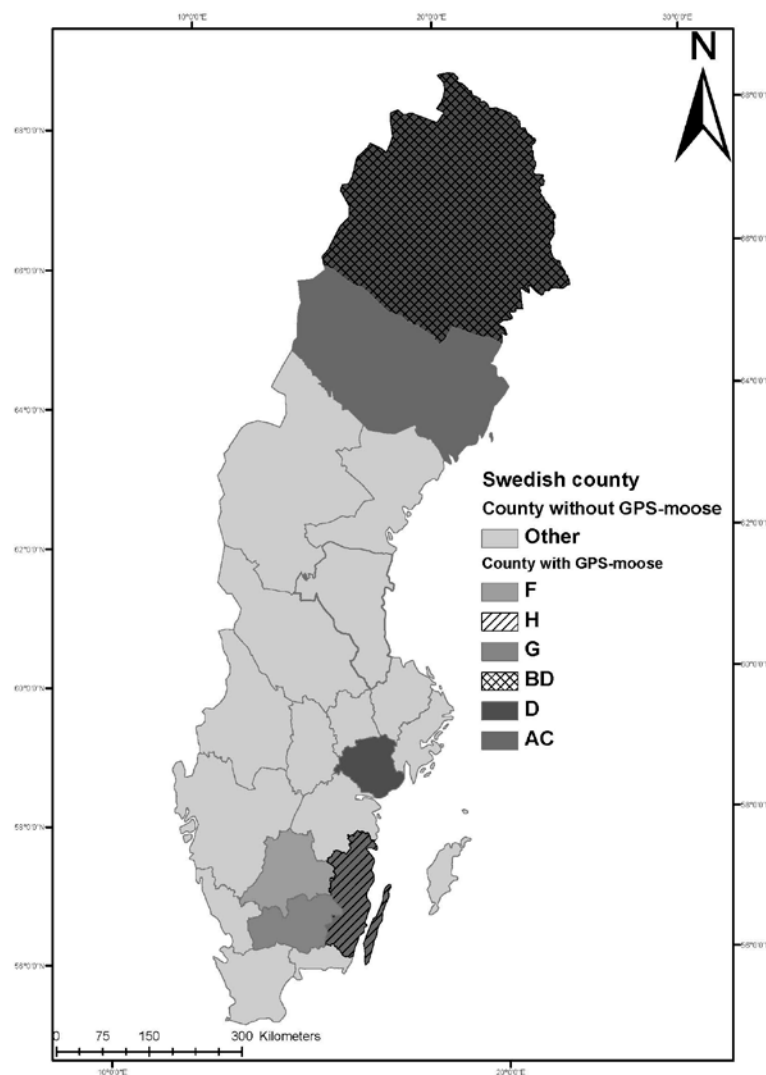


Figure 3. Map of Sweden with study areas where the data for this study were collected are highlighted. © Lantmäteriet, i2012/901.

Data preparation

The moose GPS tracking data were collected from 408 moose from Västerbotten (AC), Norrbotten (BD), Kronoberg (G), Kalmar (H), Södermanland (D) Jönköpings (F) counties (Figure 3) during the years from 2004-2011. The moose were darted during winter from helicopter and immobilized and fitted with a Global Positioning System (GPS) collar (Vectronic Aerospace GmbH, Berlin, Germany). The GPS units were pre-set to fix a position each 5 min, 30 min, 1 or 2 hours, the unit contains a Global System of Mobile communication (GSM) transmitter to send the positions of the moose in Short Messages Service (SMS) each 3.5 hours (Dettki et al. 2004). The data were transmitted to Wireless Remote Animals Monitoring (WRAM) at Swedish University of agriculture sciences (SLU) Umeå and joined to individual ID numbers. The database was accessed with Microsoft Access 2010 and subset with relocation data with one position per day for the seasonal range estimation and one relocation each second hour for the stopover/rut site estimation. All statistical analyses were carried out in R (R core Team, 2012) or Excel 2010. For an overview of the entire process see figure 5.

Individual level

Seasonal Range

The estimation of summer and winter ranges was done with one GPS point each day at 12:00. Following the method to create moose years in Singh et al. (2012) the year started by the 21 of March when all animals were located at their wintering areas and all moose with less than 330 GPS fixes was removed. A total of 223 individuals were left. Selection of data were done in R with all individual moose with more than 365 fixes were selected; this left a total of 177 moose. In this way I got the individuals that had both relocations year one and the following year.

Calving site

To determine the calving sites, the GPS positions were studied and checked for “calving clusters” (Figure 4), a place where the GPS positions are closely clustered together during May or June. These points are closer together than usual activities such as browsing. Most of the calving clusters were visited in the field to confirm the calving (>60%). The centroid of the clusters was then calculated and the GPS positions for the centroids were used in the future estimation of the calving site fidelity. A total of 405 moose calving sites have been recorded from 2004-2012. Of these 169 confirmed calving locations were used in the following estimation. The calving sites came from 67 different females that had at least two years of calving locations.

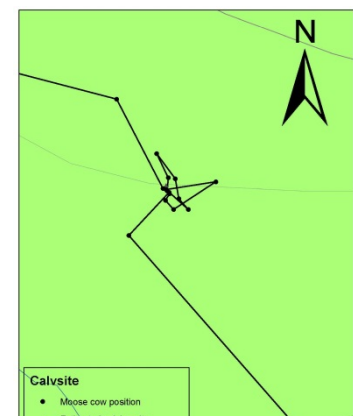


Figure 4. Calving cluster of moose, aa_ac_04_028, year 2007.

Fall and spring stopover sites

The data used for the fall and spring stopover site fidelity was estimated by using a GPS fix every second hour. The spring and autumn migration paths were determined using kernelUD a tool to estimate animals home ranges from points in ArcGIS (ESRI 2011) and the 95% percentiles were used to estimate the seasonal ranges. Those were then removed and the

area between two ranges was used to determine the start and end of migration, for further information see (Lindberg 2013). This selection gave a total of 44 individual moose that had a total of 87 moose-years all in the Västerbotten area.

Rutting site fidelity

I used 165 calving dates and calculated a mean for both the south and the north population. I then back calculated from the mean date 231 days, the mean gestation time for moose (Schwartz & Hundertmark 1993). I then selected 18 moose from north during September and 9 moose from the south during October with the high resolution data. This gave a total of 98 moose-years,

Data Analyses

Individual level

I used a kernelbb estimation to estimate the seasonal ranges as well as fall and spring stopover utilisation distributions (UD) and the rutting areas UD. The kernelbb is basically a Brownian bridge movement model (BBMM) introduced by Horne et al. (2007) and included in the adehabitatHR package in R (Calenge 2006). The home range estimation is dependent on two variables sig1 and sig2. The sig1 value is related to the movement speed of the animal while the sig2 value relates to the measurement error from the GPS fixes. The input needed to create a UD in kernelbb is given in Table 1.

To calculate the individual sig1 value I used the function #liker. In the estimation I used the following settings for the seasonal range estimation: rangesig1 = 1 to 10, sig2 = 10 and le-value of 500. In the stopover estimations I used: rangesig1 = 1 to 50, sig2 = 10 and le-value of 500, the same values were used in the estimation for the rut areas.

Table 1. The model parameters used in the UD estimations from the Brownian Bridge Movement Model for estimating home ranges.

Kernelbb input			
	Seasonal range	Stopover sites	Rut area
Ltraj(a line object with the time, ID and Coordinates)	Moose data(1 fix/day) Time, ID and Coordinates	High resolution data(12fix/day) Time, ID and Coordinates	High resolution data(12 fix/day) Time, ID and Coordinates
Sig1(movement speed)	Created from liker	Created from liker	Created by liker
Sig2	10	10	10
Grid	200	400	450
Extent	0,0001	0,00001	0,00001

Seasonal Range

The moose were sorted into groups by the marking latitude from 56°(N=5), 57°(N=29), 65°(N=58), 66°(N=69), 67°(N=16) (from here on called 56,57,65,66,67). I then divided the year into summer and winter, based on the dates of onset of spring and autumn migrations, this to be able to estimate the seasonal UD. After splitting the data into the two seasons I performed the steps needed to run kernelbb estimation, this produced a total of 286 seasonal moose-years UD. These were then put into the kerneloverlaphr function.

Stopover sites

I created the stopover UD with the same function but I used the settings given in Table 1 to create the UD. This gave a total of 82 and 83 different moose-years with spring and fall stopover sites UD respectively, the fall and spring stopover site for one moose can be seen in Appendix 1. Overlap among these sites was then estimated using the kerneloverlaphr function in R.

Rutting sites

To estimate the UD of the rutting sites I used the kernelbb function with the data selection from table 1. This produced 31 and 67 moose-years for the southern and northern populations respectively, the rutting sites of two moose, one in the south and one in the north can be seen in Appendix 2.

Overlap

The overlap of both summer and winter seasonal range, the stopover sites and the rutting sites was calculated using the kerneloverlaphr function in R with the BA extension that is based on Bhattacharyya's affinity calculation (Fieberg & Kochanny 2005, See Equation 1).

$$BA = \frac{\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{UD_1(x,y)} * \sqrt{UD_2(x,y)} dx dy}{\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \sqrt{UD_1(x,y)} * \sqrt{UD_2(x,y)} dx dy} \quad \text{Equation 1.}$$

Where BA is the overlap in percent ranging from 0 (no overlap) to 1 (total overlap). The \widehat{UD}_1 is the utilization distribution for first year of home range estimate containing the coordinates(x,y) and \widehat{UD}_2 is the second year's home range estimation. This method has been tested by Fieberg and Kochanny (2005) and provides a good estimate of the overlap between area calculations. I looked at the 50 and 90 percent contours for the seasonal range and rut site overlap, and for the stopover site only the 50 percent contour overlap.

The kerneloverlaphr function produced a matrix with overlaps of the UD from one individual to all the rest present in the test. I then selected the overlap from year i to year i+1 and put them in a new data frame to calculate the populations characteristics. The result was divided by 0, 5 or 0.9 to get the overlap on a 100% scale.

Calving sites

The calving site data was divided into groups based on their latitudes in the same way as the seasonal ranges. This dataset was used to look at individual calving site fidelity. The distance between two consecutive calving sites was calculated using Euclidian distance (see Equation 2)

$$d(a,b) = \sqrt{(a_x - b_x)^2 + (a_y - b_y)^2} \quad \text{Equation 2.}$$

Where a and b are two points with a latitude(x) and a longitude(y) value. The Euclidian distance was then used to determine if calving site fidelity was present. I got 82 distances between individual calving sites over consecutive years. Site fidelity was present when consecutive calving sites were <1000 meters from each other (Welch et al. 2000, Wiseman et al. 2006). The calving distance data is presented with the County letters to separate them from the calculations of overlap.

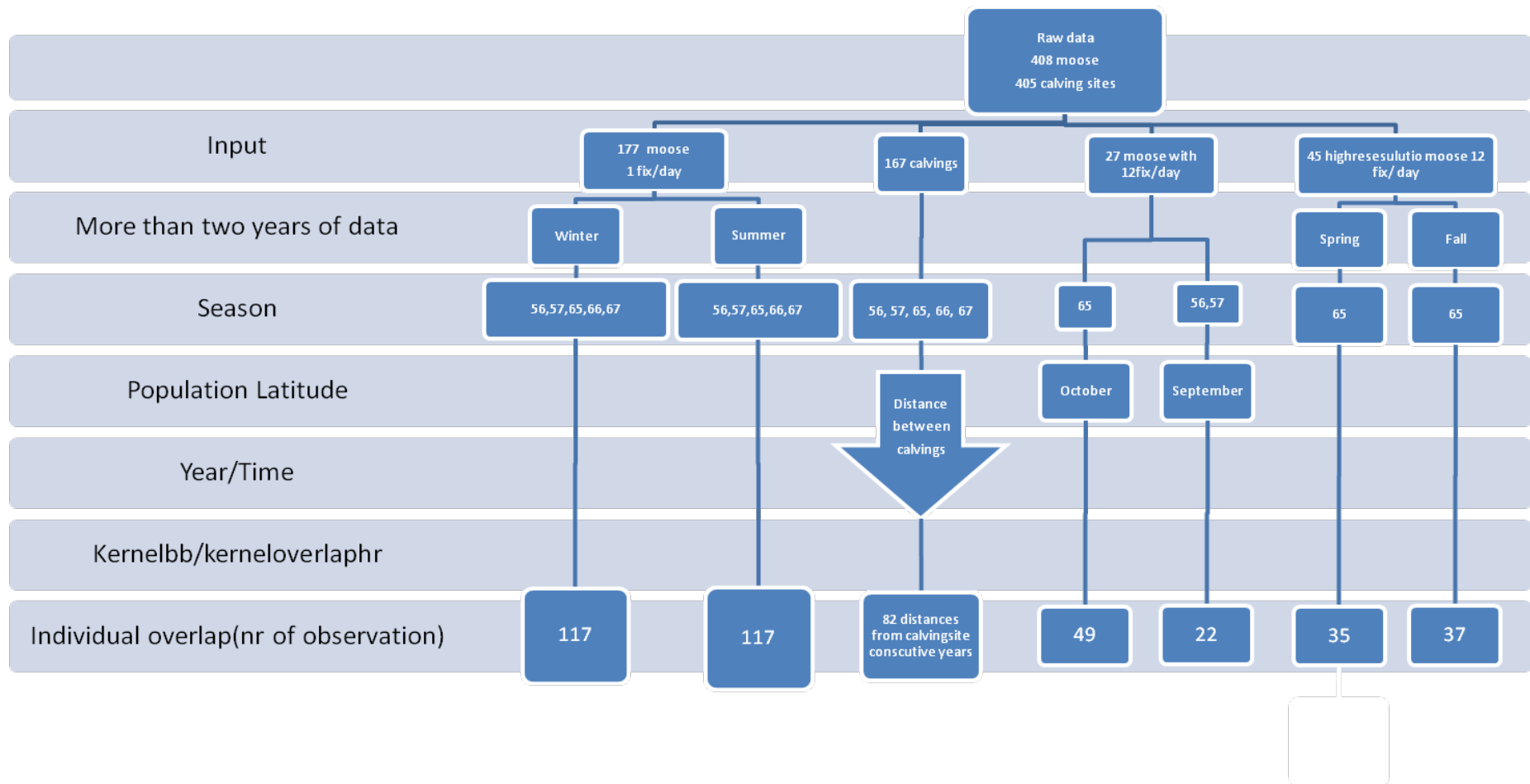


Figure 5. Flow chart of the process, input and the output on the individual overlap and calving distances in the studie.

Results

Seasonal Range

The size of the seasonal ranges varied from south to north with the largest areas occurring in the fourth latitudinal group (66, Figure 6) both in winter and summer. The smallest summer ranges was found in one of the more southern latitudinal group, 56.

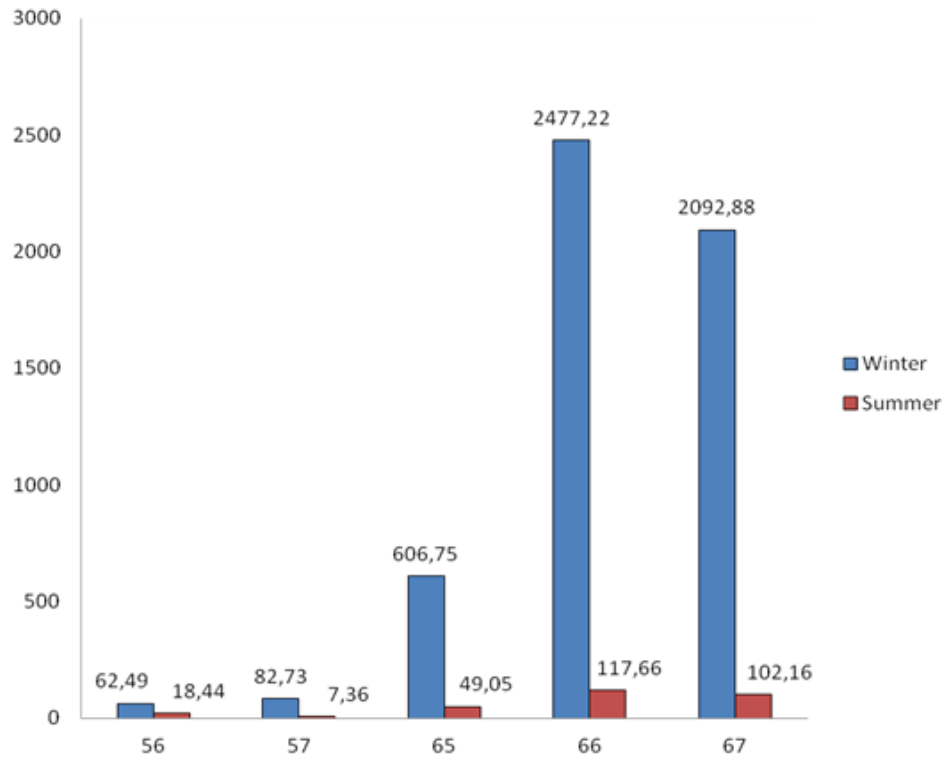


Figure 6. Size of seasonal ranges in km² of the 90% UD_s during summer and winter from south to north.

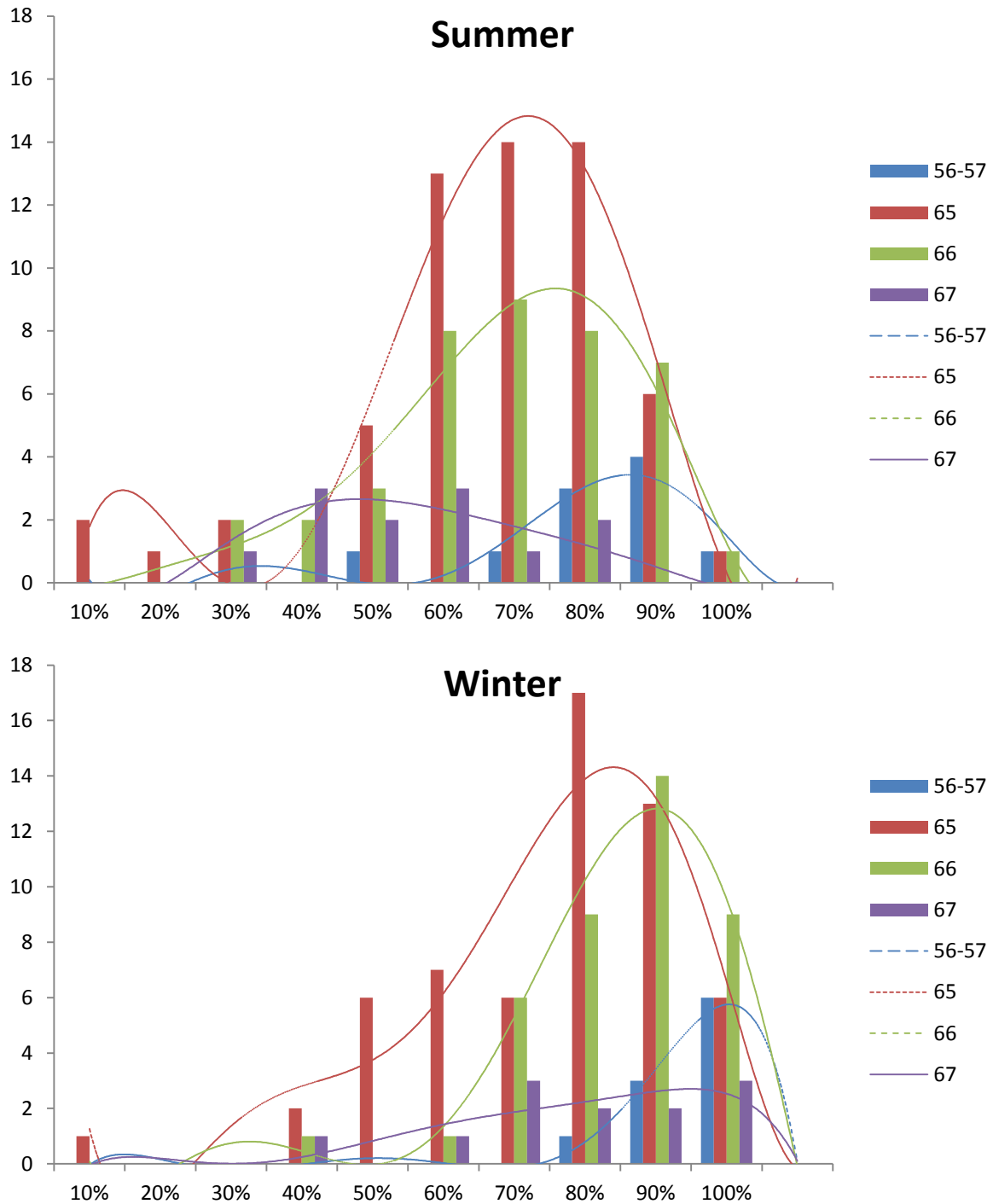


Figure 7. Individual overlap from year i to $i+1$ in both summer and winter range, number of observations on y- axis and the percentage of overlap on the x- axis. Polynomial lines show the weight of the population's fidelity.

The fidelity to summer areas is highest in the most southern population followed by the 66 and the 65 (Figure 7, Summer). The lowest fidelity to the summer range was seen in the 67 population. In the summer range a wider pattern of fidelity was seen with some animals showing low fidelity while other showed a higher degree of it, in the same population.

In the winter range the southern populations showed the highest degree of fidelity followed by the most northern population and then a decrease was seen by latitude (See Figure 7, Winter). During winter the fidelity was higher and also the level of fidelity was more concentrated in each population.

Calving site

The mean timing of calving throughout Sweden differed by approximately one month (Table 3), the calving period was due by one month. There were no large differences in the start or the end dates of the calving between years.

Table 3. Mean calving date in the north and in the southern part of Sweden as well as number of calvings in each latitudinal group. Västerbotten (AC), Norrbotten (BD), Kronoberg (G), Kalmar (H), Södermanland (D) Jönköpings (F) counties.

					Calving sites per County				
	Year	Birth,min	Birth,max	Mean date	AC	BD	H	G	D
North	2005	23-maj	23-jun	05-jun	13				
	2006	27-maj	14-jun	04-jun	23				
	2007	25-maj	10-jun	02-jun	13				
	2008	25-maj	19-jun	05-jun	15	1			
	2009	30-maj	11-jun	04-jun	7				
South	2009	04-maj	26-jun	13-maj				13	2
	2010	08-maj	03-jun	18-maj			7	16	5
	2011	10-maj	31-maj	18-maj			7	11	3
	2012	01-maj	12-jun	13-maj			5	12	2

Calving site fidelity was present in all latitudinal groups but the more southern group had a higher degree of it (Table 4). In all areas the closest calving site from consecutive years was ≤ 100 meters from the previous year (Table 4).

Table 4. The mean, SE and number of observations of Euclidian distances from calving year i to $i+1$ in the different latitudinal groups from south to the north. Västerbotten (AC), Kronoberg (G), Kalmar (H), Södermanland (D) counties.

	G,H	D	AC
Mean(m)	1251,0	2395,3	15899,0
SE(m)	159,8	1750,3	3861,7
N	37	7	38

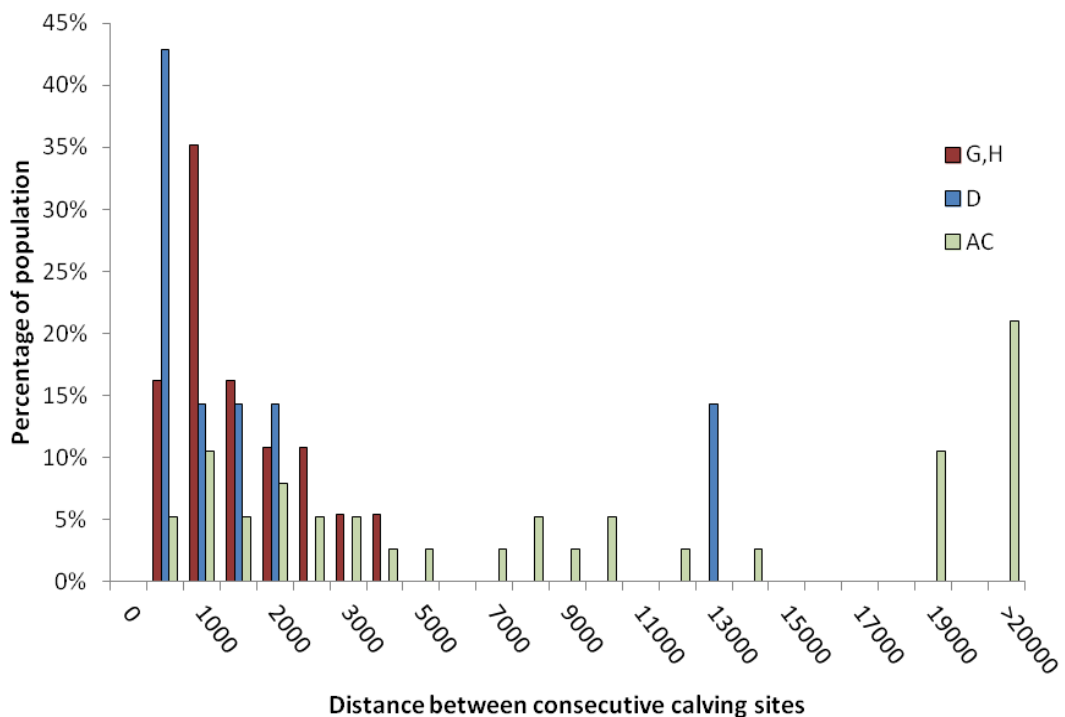


Figure 8. The distance between consecutive years of calving sites with the percentage of observation found in the different ranges at the three different latitude groups.

In the southern Sweden 51% of the individuals calved ≤ 1000 m from the previous year's calving site, a distance that could imply site fidelity (Figure 8, G, H) (Welch et al. 2000; Wiseman et al. 2006). In central Sweden an even higher degree of fidelity was seen, 57% of the observed distances between individual calving sites from year i to year $i+1$, indicate strong fidelity (Figure 8, D). Fifteen percent of the populations in the northern part of Sweden showed fidelity from year i to year $i+1$ (Figure 8, AC).

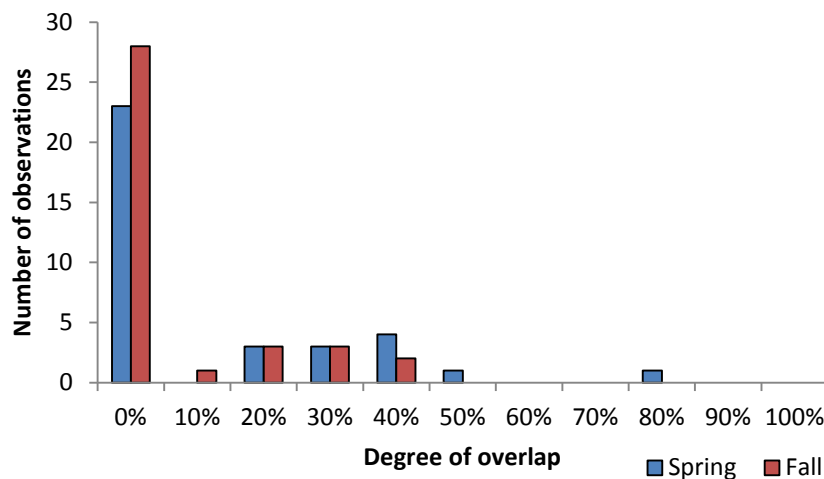


Figure 9. Number of observations in each percentage class of overlap on the stopover site in Västerbotten (AC) County.

Stopover sites

Fidelity to fall stopover sites was low and over 70% of the observations showed no fidelity to the stopover sites during the fall migration (Figure 9). During the spring migration a small portion of the migratory individuals showed site fidelity. A few observations showed a very high degree of overlap, but more than 60% of the individuals showed no fidelity during the spring (Figure 9).

Rutting sites

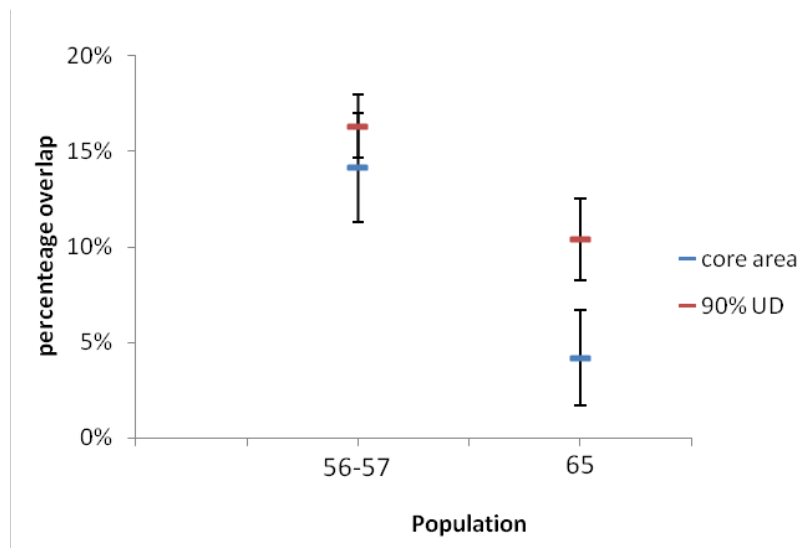


Figure 10. The mean and SE overlap of the south and north populations (represented by latitude value) in the core areas and the 90% UD.

The mean range overlap during the rut was small (Figure 10) and decreased from the south to the north.

Discussion

The large dataset with information from the different parts of the landscape provide a broad base to look at fidelity along a latitudinal gradient in Sweden. Fidelity in the Swedish moose population is seen on all levels from calving sites to seasonal range. My key findings are that site fidelity in the south of Sweden is very high year round. During winter the fidelity too winter ranges is high with a gradient from the 67 to the 65th population. Linking the observed fidelity to the different movement strategies creates a picture where migratory animals show fidelity during winter and sedentary animals show fidelity on a year round basis. The calving site fidelity shows a clear gradient in accordance to the third prediction and is most affected by anthropogenic risk.

Seasonal Range

In all the different latitudinal groups and by all the individuals I found fidelity to the seasonal range, the same pattern was seen by Cederlund et al. (1987). The level of individual overlap between years was always over 25%. Fidelity was as predicted high both in the most northern populations during winter and year round in the most southern population, this in accordance with prediction 1 and 2. This has probably many causes but as mentioned before the high levels of anthropogenic risk of southern Sweden in combination with food availability, which in turns leads to smaller ranges, could be one explanation. Further a larger part of the population shows a more sedentary movement strategy which could be expected to show a higher level of fidelity (Singh et al. 2012).

In the north of Sweden an increase of fidelity in the winter range can be seen. This is in line with the second prediction. The mean re-use of areas on the individual level was around 80%. As snow makes large areas of the home ranges inaccessible during winter the moose will need to select for areas with high quality of browsing but also areas where snow condition is good.

Calving site

Fidelity in the southern latitudinal groups, Kronoberg (G), Kalmar (H) and Södermanland (D) was high, with more than 50% of the observations showing signs of fidelity. The Södermanland (D) area has a population of large predators which have the ability to kill moose (Odden et al. 2006), but in the Västerbotten (AC) county where only bears are present (Swenson et al. 2006) the fidelity is low, hence both inline and not with the third prediction. This leads to the conclusion that anthropogenic disturbance might be the driving force behind the high fidelity to calving sites in southern counties (Ciuti et al. 2012). I found higher degree of site fidelity in the southern latitudinal groups than reported before in both Scandinavia and Alaska (Tremblay et al. 2007, Welch et al. 2000). The Västerbotten (AC) population showed a more similar pattern to the Norwegian study done by Tremblay et al. (2007). Given the high degree of fidelity in the south the importance of calving areas to the moose in the southern part of Sweden is crucial. The calving sites are selected by moose females to trade-off food versus security and to find food to cope with the birth and the time after. This behaviour affects the survival and further the fitness of the moose. The interaction with humans is greater in the south than in the north (Lavsund et al. 2003). The high fidelity could be in response to predation risk as seen by Welch (et al. 2000) and Tremblay (et al. 2007) or due to human disturbance. To see the effects of large carnivores on site fidelity there is a need to have more information on how they interact with moose and how the moose respond to the presence of different carnivores.

Fall and spring stopover sites

Little overlap was seen in the fall stopover areas at an individual level. The start and stop of the fall migration is most likely determined by the arrival of snow, which can be variable from year to year. This could be the reason behind the low fidelity to stopover sites, as the location of a moose may vary from year to year due to snow conditions. Similarly, the fidelity towards spring stopovers was low and most likely due to a similar reason, where the onset of spring may determine the start of migration and hence the location of moose in the landscape.

Rutting sites

There was low fidelity to rutting sites in both the northern part of Sweden and the southern part, yet the southern latitude group showed a higher degree of fidelity than the northern one. Why the pattern of low fidelity is seen to rutting sites can have many causes, one of them might be that of the movement caused when males chase females around on the rutting site (VanBallenberghe & Miquelle 1996). Another reason could be that of hunting, as hunting pressure can be high during the rutting period and thus some animals might move more to avoid hunters (Neumann et al. 2009). Another reason might be that the high densities inhibit the animals to aggregate a behaviour seen in more undisturbed areas (VanBallenberghe & Miquelle 1996).

Method development

The kernelbb used to estimate the utilization distributions in all the different steps but the calving site fidelity, has not prior to this been used on these large samples sizes (Calenge 2006, Durmus 2010). The BBMM method should be able to handle a great amount of relocations and produce a good estimate if the time lag between relocations is equal (Horne et al. 2007). However, the method struggled to handle a large number of individuals; leading to enormous amount of time spent in calculations and sometimes produced errors which were incomprehensible. The use of Euclidian distance to calculate site fidelity is simple but may lack in precision, as the estimation does not take in account the complexity of the landscape or other factors like movement pattern of the moose and the abundance of suitable calving habitat (Welch et al. 2000). Despite this it has been used frequently too look at calving site fidelity (Wiseman et al. 2006; Welch et al. 2000).

Limitations

Due to time limitations, I was not able to model the factors that determine site fidelity and have mostly speculated the reasons based on the maps included. The next immediate step is to model the factors that predict the range overlap observed at different levels of the study and also the differences in distances between the calving sites in the consecutive years.

Conclusions

Fidelity to the summer and winter range was high in all the different populations. The sedentary southern population showed a year around high fidelity. In the north there were a gradient in fidelity from the 67th to the 65th population during winter with the highest fidelity in the most northern population. These results further build on the predictions that knowledge of where to find high quality browsing in combination with a safe haven from

predators may increase site fidelity. Calving site fidelity was high in the two southern populations where anthropogenic disturbance might be one of the heaviest reasons behind the calving site fidelity. Fidelity to stopover sites was low, this is probably due to food availability and the unpredictability of the greening up in spring. Rutting site fidelity was low, this could probably be due to high abundance of moose as the moose don't need to aggregate to find mates, or the rutting behaviour of males chasing females around. Working with animals showing different kinds of fidelity, the scale of the estimation becomes very important. As the choice of scale will lead to different results, the need to find the right scale to look at fidelity is vital. The range size and the different movement strategies of the animal are important information in the prediction of site fidelity.

Management applications

Fidelity is present in all the different moose populations, this knowledge could be implemented in the new moose management system of Sweden, to set better quotas and to better predict the response of hunting in certain areas. The results also show that there is a clear pattern with an increase of fidelity from the south to the north during winter that can be linked to the different movement strategies, but also the range size. It also shows that in the most southern part of Sweden the same view cannot be used to manage or conserve the moose, as they do not behave in the same way as in the north; this might be because of high numbers. Given the high degree of fidelity in the south, the importance of calving areas to the moose in the southern part of Sweden is crucial. As the calving sites are chosen by the moose cows to have the supplies that are needed to cope with the birth and the time after. This behaviour affects the survival and further the fitness of the moose. The large data set provides a good base to look at fidelity in different latitudinal groups. Today few individuals are marked in the central part of Sweden, giving a gap in the data. This region could give a more complete picture if the data was available.

Acknowledgments

I would like to thank my supervisor Dr. Navinder J, Singh, and co-supervisor Prof. Göran Ericsson for the support and the challenges. Furthermore, I would like to thank my fellow forestry students that have come with comments and help to make the picture clearer. A special thanks to Jens Lindberg that have been working alongside me on the moose data and has contributed with valuable insights.

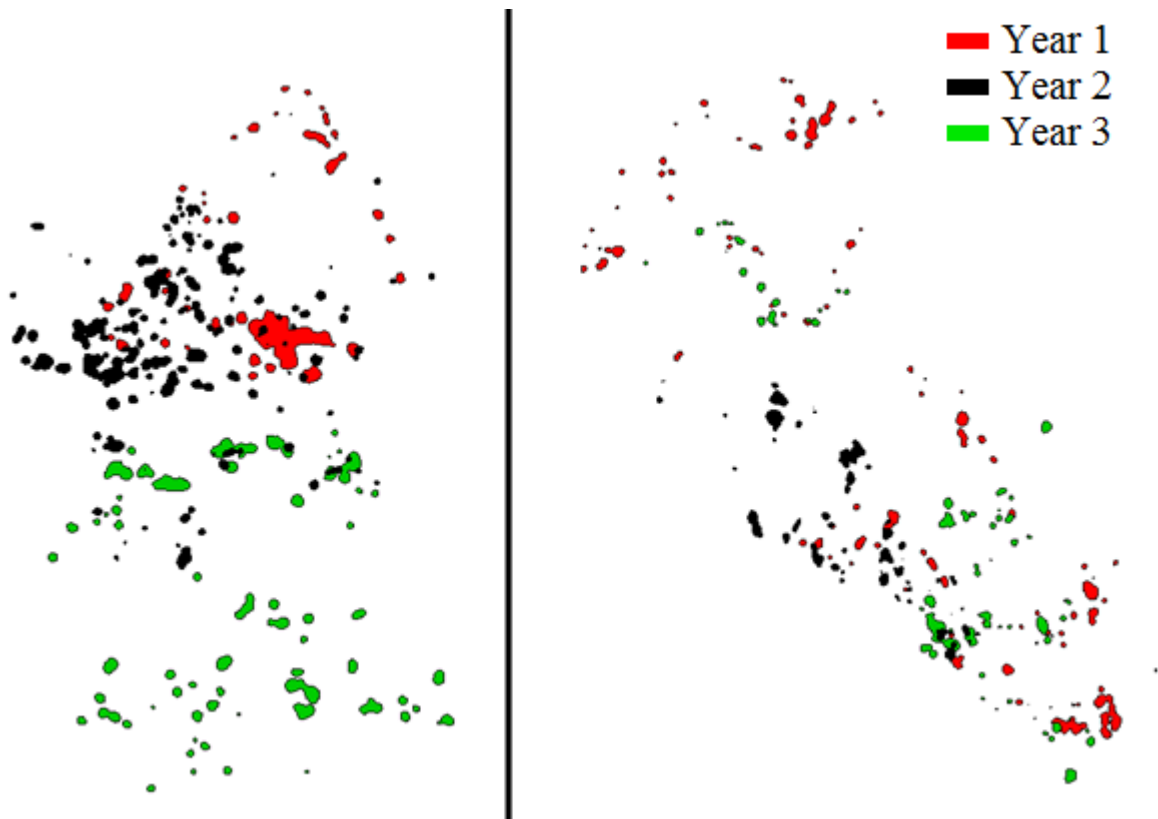
References

- Bolger, D., T., Newmark, W., D., Morrison, T., A., Doak, D., F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology letters* 11: 63-77.
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F., Godley, B. J. (2007). Fidelity and over-wintering in sea turtles. *Proceedings of the Royal society* 274: 1533-1538.
- Buchanan, J. B., Lyons, J. E., Salzer, L. J., Carmona, R., Arce, N., Wiles, G. J., Brady, K., Hayes, G. E., Desimone, S. M., Schirato, G., Michaelis, W. (2012). Among-year site fidelity of Red Knots during migration in Washington. *Journal of field ornithology* 83: 282-289.
- Calenge, C (2006). Exploring habitat selection by wildlife with adehabitat. *Journal of statistical software* 6: 2007.
- Cameron, R. D., Reed, D. J., Dau, J. R., Smith, W. T. (1992). Redistribution of calving caribou in response to oil field development on the arctic slope of Alaska. *Arctic* 45: 338-342.
- Cederlund, G., Sandegren, F., Larsson, K.(1987). Summer movements of female Moose and dispersal of their offspring. *Journal of wildlife management* 51: 342-352.
- Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., Boyce, M. S. (2012). Effect of humans on behavior of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE* 7:1-13.
- Dettki, H., Ericsson, G., Edenius, L. (2004). Real-time moose tracking: an internet based mapping application using GPS/GSM-collars in Sweden. *Alces* 40: 13-21.
- Durmus, M.(2010) Determination of home range size and habitat selection of gazelles(*Gazella subgutturosa*) by GPS telemetry in Sanliurfa. Master of Science in department of biological sciences, Middle East technical university.
- Esler, D.(2000). Applying metapopulation theory to conservation of migratory birds. *Conservation biology* 14: 366-372.
- ESRI (Environmental Systems Resource Institute). (2011). ArcMap 10. ESRI, Redlands, California.
- Faille, G., Dussault, C., Ouellet, J.-P., Fortin, D., Courtois, R., St-Laurent, M.-H., Dussault, C. (2010). Range fidelity: The missing link between caribou decline and habitat alteration? *Biological Conservation* 143: 2840-2850.
- FAO. Homepage [Online](2013-04-07). Available from: <http://www.fao.org/forestry/country/32185/en/swe/>
- Fieberg, J. & Kochanny, C. O.,(2005). Quantifying home-range overlap: the importance of the utilization distribution. *Journal of wildlife management* 4: 1346-1359.
- Furmankiewicz, J., Altringham, J.(2007). Genetic structure in a swarming brown long-eared bat(*Plecotus auritus*) population: evidence for mating at swarming sites. *Conservation genetic* 8: 913-923.
- Fryxell, J. M., Greever, J., Sinclair, A. R. E.(1987).Why are migratory ungulates so abundant? *The American naturalist* 131: 781-798.
- Greenwood, P., J. (1980). Mating systems, Philopatry and dispersal in birds and mammals. *Animal behaviour* 28: 1140-1162.
- Haydn, A. (2012). Calving site selection by moose (*Alces alces*) along a latitudinal gradient in Sweden. Master degree thesis in biology at the department of Wildlife, Fish and Environmental Studies.
- Horne, J. S., Garton, E. O., Krone, S. M., Lewis, J. S. (2007). Analyzing animal movement using Brownian bridges. *Ecology* 88: 2354-2364.

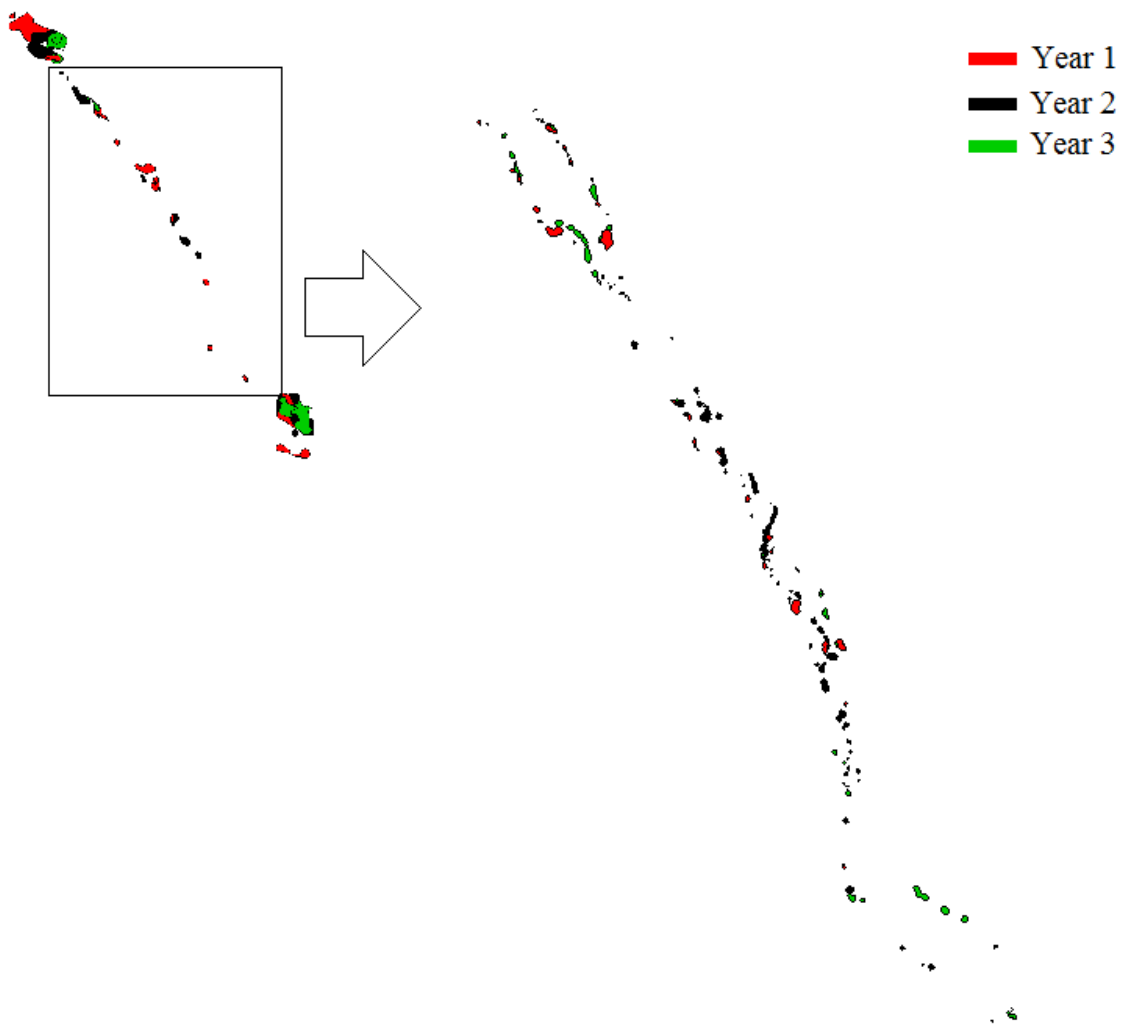
- Irons, D., B. (1998). Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647-655.
- Jensen, B. 2004. Nordens pattedyr 2nd edition. Gyldendalske boghandel. Köpenhamn.
- Lavsund, S., Nygrén, T., Solberg, E. J.(2003). Status of moose populations and challenges to moose management in Fennoscandia. *Alces* 39: 109-130.
- Lindberg, J.(2013). Selection of habitat and resources during migration by a large mammal- A case study of moose in northern Sweden. Master degree thesis in biology at the department of Wildlife, Fish and Environmental Studies.
- Maier, J., A., K., Ver Hoef, J., M., McGuire, D., A., Bowyer, T., R., Saperstein, L. Maier, A., H., (2005). Distribution and density of moose in relation to landscape characteristics: effect of scale. *Canadian journal of forest research* 35: 2233-2243.
- Morrison, A. T. and Bolger, T. D.(2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of animal Ecology* 81: 543-552.
- Muller, T., Olson, K. A., Fuller, T. K., Schaller, G. B., Murray, M. G., Leimgruber, P. (2007). In search of forage: predicting dynamic habitats of mongolian gazells using satellite-based estimates of vegetation productivity. *Journal of applied ecology* 2007: 1-11.
- Muller, T., Olson, K. A., Dressler, G., Leimgruber, P., Fuller, T. K., Nicolson, C., Novaro, A. J., Bolgeri, M. J., Wattles, D. DeStefano, S., Calabrese, J. M., Fangan, W. F.(2011). How landscape dynamics link individual- to population –level movement patterns: a multispecies comparison of ungulate relocation data. *Global ecology and biogeography*: 1-12.
- Norbury, G. L., Norbury, D. C., Oliver, A. J.(1994). Facultative behavior in unpredictable environments: mobility of red kangaroos in arid western Australia. *Journal of animal ecology* 63: 410-418.
- Neumann, W., Ericsson, G., Dettki, H.(2009). The non-impact of hunting on moose Alces alces movement, diurnal activity, and activity range. *European journal of wildlife research* 55: 255-265.
- Neumann, W., Ericsson, G., Dettki, G., Bunnefeld, N., Keuler, N., S., Helmers, D., P., Radeloff, V., C. (2012). Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. *Biological conservation* 145: 70-78.
- Odden, J., Linnell, J. D. C., Andersen, R.(2006). Diet of Eurasian lynx, Lynx lynx, in the boreal forest of southern Norway: the relative importance of livestock and hares at low roe deer density. *European journal of wildlife research* 52: 237-244.
- Persson, I.-L. (2003). Moose population density and habitat productivity as drivers of ecosystem processes in northern boreal forests. *Doctoral dissertation (ISBN 91-576-6506-0)*
- Pomeroy, P. P., Twiss, S. D., Redman, P. (2000). Philopatry, site fidelity and local kin associations within grey seal breeding colonies. *Ethology* 106: 899-919.
- Riksskogstaxeringen. Home page [Online](2013-02-17). Available from: <http://www.slu.se/sv/webbtjanster-miljoanalys/statistik-om-skog/arealer/>
- R Core Team. (2013). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria, Homepage [Online], <http://www.R-project.org>.
- Sahlsten, J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., Dettki, H. (2010). Can supplementary feeding be used to redistribute moose Alces alces? *Wildlife biology* 16: 85-92.

- Sawyer, H., Kauffman, M., J., Nielson, R., M., Horne, J., S. (2009). Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological applications* 19: 2016-2025.
- Sawyer, H., Lebeau, C., Hart, T. (2012). Mitigating roadway impacts to migratory mule deer – A case study with underpasses and continuous fencing. *Wildlife society bulletin* 36: 492-298.
- Schieck, J. O., Hannon, S. J. (1989). Breeding Fidelity in willow Ptarmigan: The influence of Previous Reproductive Success and Familiarity with partner and territory. *Oecologia* 81: 465-472.
- Schroeder, M. A., Robb, L. A. (2003). Fidelity of greater sage-grouse (*Centrocercus urophasianus*) to breeding areas in fragmented landscape. *Wildlife Biology* 9: 291-299.
- Schwartz, C. and Hundertmark, K. (1993). Reproductive characteristics of Alaskan moose. *Journal of wildlife management* 57: 454-468.
- Singh, N., J., Grachev, I., A., Bekenov, A., B., Milner-Gulland, E., J. (2010). Siaga antelope calving site selection is increasingly driven by human disturbance. *Biological conservation* 143: 1770-1779.
- Singh, N., J., Börger, L., Dettki, H., Bunnefeld, N., Ericsson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological application* 22: 2007-2020.
- Skogsstyrelsen (2012). Skogsstatistisk årsbok 2012[pdf] Rapport, Jönköping, Skogsstyrelsen. Available from: <http://www.skogsstyrelsen.se/sv/Myndigheten/Statistik/Skogsstatistisk-Arsbok/Skogsstatistiska-arsbocker/>
- SMHI. Homepage [Online] (2013-02-17). Available from: <http://www.smhi.se/kunskapsbanken/sverigemedeltemperatur-1.21151>
- Sweaner, P. Y. and Sandegren, F. (1989). Winter-range philopatry of seasonally migratory moose. *Journal of Applied Ecology* 26: 25-33.
- Swenson, J. E., Dahle, B., Busk, H., Opseth, O., Johansen, T., Söderberg, A., Wallin, K., Cederlund, G. (2006). Predation on moose calves by European brown bears. *The journal of wildlife management* 71: 1993-1997.
- Switzer, P., V. (1993). Site fidelity in predictable and unpredictable habitats, *Evolutionary Ecology* 7: 533-555.
- Taylor, A. R. and Bishop, M. A. (2008) Stop over site fidelity of a western sandpiper on the copper river delta, Alaska. *Waterbirds* 31: 293-297.
- Thompson, I., D. & Vukelich, M., F. (1981). Use of logged habitats in winter by moose cows with calves in northern Ontario. *Canadian journal of Zoology* 59: 2103-2114.
- Tremblay, J.-P., Solberg, E. J., Saether, B.-E., Heim, M. (2007). *Canadian journal of zoology* 85: 902-908.
- VanBallenberghe, V. and Miquelle, D. G. (1996). Rutting behavior of moose in central Alaska. *Alces* 32: 109-130.
- VanBeest, F. M., Mysterud, A., Loe, L. E., Milner, J. M. (2010). Forage quantity, quality and depletion as scale dependent mechanisms driving habitat selection of a larger browsing herbivore. *Journal of Animal Ecology* 79: 910-922.
- Welch, I. D., Rodgers, A. R., McKinley, R. S. (2000). Timber harvest and calving site fidelity of moose in north western Ontario. *Alces* 36: 93-103.
- Wiseman, P. A., Carling, M. D., Byers, J. A. (2006). Frequency and correlates of birth-site fidelity in pronghorns (*antilocapra americana*). *Journal of mammalogy* 87: 312-317.

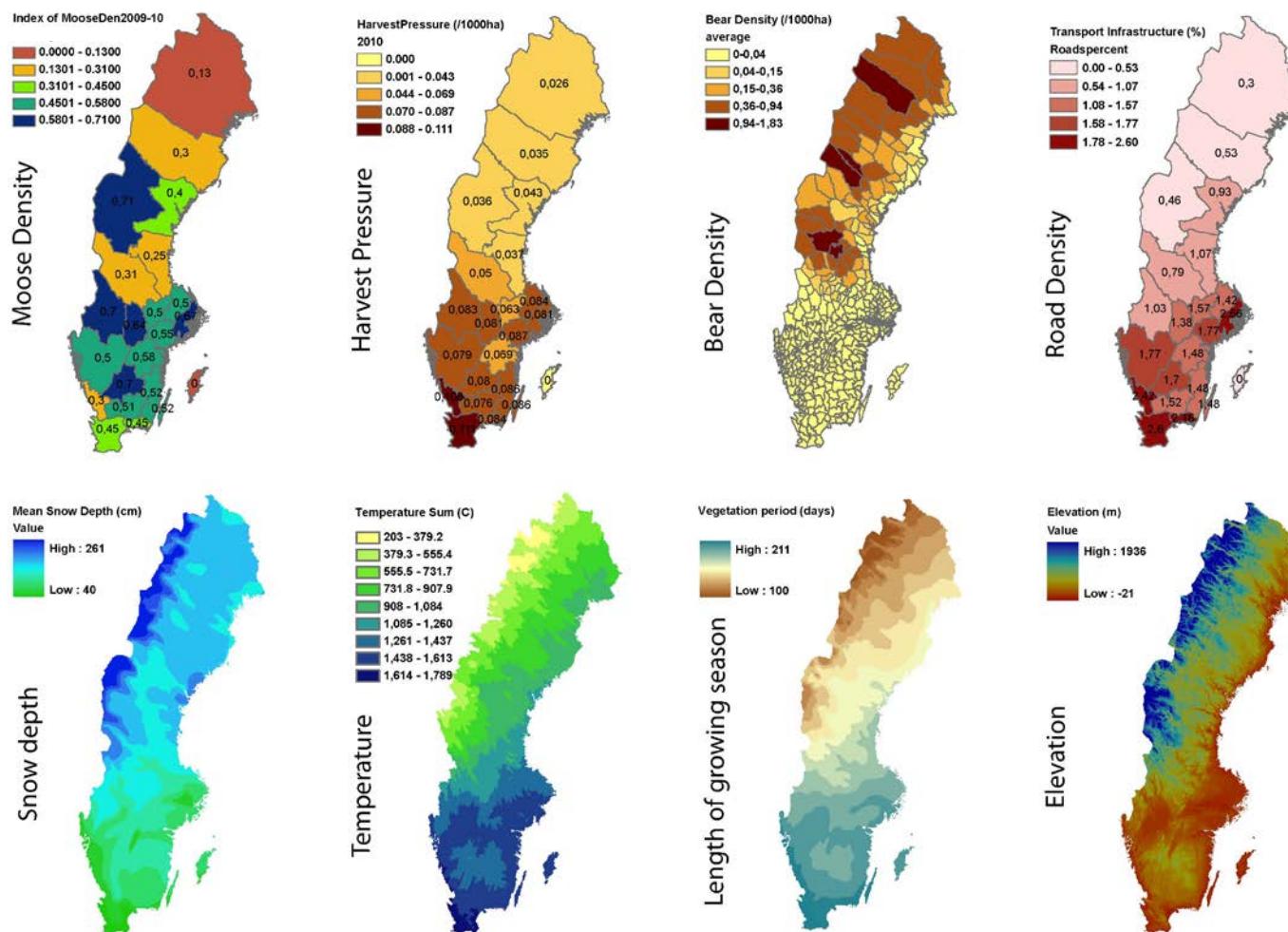
Appendix



Appendix 1. Three years of 50 % UD_s during the rutting period, to the left, aa_g0_09_005 in the south of Sweden and aa_ac_04_028 to the right from the north of Sweden.



Appendix 2. Stopover sites for moose aa_ac_04_028 during 3 years of both spring and fall migration, the animal belongs to the 65 latitude group.



Appendix 3. Covariates that influence site fidelity in the moose population of Sweden (from Singh et al. 2012).

SENASTE UTGIVNA NUMMER

- 2011:6 *De novo* sequencing and SNP discovery in the Scandinavian brown bear (*Ursus arctos*).
Författare: Anita J Norman
- 2011:7 A genetic approach to identify raccoon dog within a large native meso-carnivore community.
Författare: Dan Wang
- 2011:8 Is old forest like old forest? Patterns in abundance and species number of resident birds in old boreal forest stands in relation to stand structure and landscape context.
Författare: Ortrud Leibinger
- 2011:9 Klövviltets nyttjande av foderraps på viltåker och betespåverkan på angränsande skog.
Författare: Maria Lidberg
- 2012:1 Attityder till återintroduktion av visent i Sverige.
Författare: Axel Bergsten
- 2012:2 Viltanpassad röjning längs skogsbilvägar som en foderskapande åtgärd för älgen.
Författare: Ida Forslund
- 2012:3 Spawning site selection of brown trout in habitat restored streams.
Författare: Jonas Svensson
- 2012:4 The shift in forest and tree limits in Troms County – with a main focus on temperature and herbivores.
Författare: Kristoffer Normark
- 2012:5 Clover (*Trifolium* spp) gamefields: Forage production, utilization by ungulates and browsing on adjacent forest.
Författare: Karl Komstedt
- 2012:6 Habitat use and ranging behaviour of GPS tracked juvenile golden eagles (*Aquila chrysaetos*).
Författare: Carolin Sandgren
- 2012:7 Spatial and temporal variation in the quality of summer foods for herbivores along a latitudinal gradient.
Författare: Michaela Holá
- 2012:8 Hur livshistoriekaraktärer hos Europeisk abborre (*Perca fluviatilis* L.) påverkas av cykliska förändringar i populationsstrukturen.
Författare: Christian Andersson
- 2012:9 Neighborhood effects as a plant defence against ungulate herbivory.
Författare: Bregje Koster
- 2012:10 Comparison of bird communities in stands of introduced lodgepole pine and native Scots pine in Sweden.
Författare: Arvid Alm